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Research Article

Diversity and distribution patterns of invasive alien plant species in mainland Portugal

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Abstract

Understanding the distribution and diversity of invasive alien species is increasingly crucial to meet legal requirements and guide effective management. Portugal currently hosts a large number of invasive alien plant species, with significant environmental and socio-economic impacts. However, the distribution of most of these species across the territory and the factors driving their spread and diversity remain largely unexplored. To address this, we present the first atlas of invasive alien plants in mainland Portugal. A total of 96 terrestrial and aquatic invasive alien plants are presented, encompassing all species listed under Portuguese national legislation and the European Union's list of invasive species of concern. Occurrence data were collected from a broad array of sources, including national and international biodiversity observation databases, citizen science data, literature, and data collections owned by managers and researchers—totaling approximately 85,000 records, with a mean of 879 records per species (range: 1–9,190). Each species was characterized based on multiple distributional parameters, and a k-means analysis was used to group species with similar distribution patterns. The richness of invasive plants was mapped at the municipality level. The drivers of their spatial variation were investigated using a comprehensive set of 30 variables representing multiple environmental and human factors. Results show that invasive plants are present in all mainland Portuguese municipalities but with high variability. Four main patterns of distribution were identified: species primarily located along the coast (e.g., *Acacia saligna*) and a gradient of species with narrow (e.g., *Reynoutria japonica*), moderate (e.g., *Ipomoea indica*), and wide distribution ranges (e.g., *Cortaderia selloana*). Invasive species richness was significantly higher in coastal and larger municipalities, particularly those closer to major urban centers and with a higher density of power lines. Our results provide the first comprehensive assessment of the distribution of invasive alien plants in mainland Portugal, establishing a much-needed baseline for future invasion prevention and management efforts.

Key words: Baseline distribution, drivers of invasion, invasion atlas, invasive alien plants, invasive species richness, occupancy

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Introduction

Human activities are facilitating the global movement and introduction of species beyond their native ranges (Pyšek et al. 2020; Lopez et al. 2022; Capinha et al. 2023). Currently, over 37,000 established alien species have been documented worldwide

(IPBES 2023), with approximately 200 new alien species (i.e., "exotic" or "non-native") recorded annually. Among these, alien plants constitute a significant proportion, with more than 13,000 species established outside their natural ranges (Seebens et al. 2023).

A minor portion of alien plants become invasive, causing significant and diverse negative impacts in regions of introduction. These impacts include reductions in native species diversity and abundance (Powell et al. 2011; Hansen et al. 2020; Beaury et al. 2023), disruption of key ecosystem services (Vieites-Blanco and González-Prieto 2020; Ferreira et al. 2021; Ren et al. 2021; Gallardo et al. 2024), and major economic losses affecting multiple activities, including the loss of crops and productive land (Richardson and Van Wilgen 2004; Le Maitre et al. 2011; Milanović et al. 2020; Reynolds et al. 2020; Sirbu et al. 2022). Additionally, several invasive plants pose environmental risks to human health (Rodriguez et al. 2021). Most of these impactful species have been reported in the American continent, the Asia–Pacific region, Central Asia, and Europe (IPBES 2023). In Europe, at least 7,335 alien vascular plant species have been recorded, of which 1,037 (about 14%) are considered invasive in at least one European territory (Kalusová et al. 2024).

Given the frequent severity of the observed and potential impacts, many national and regional governments now prioritize managing biological invasions, including such species in dedicated legislation. Portugal was one of the first European countries to adopt legislation on invasive alien species (hereafter invasive species), introducing in 1999 a list of species subject to specific restrictions, including bans on commercial use and possession (Ministério do Ambiente 1999). This list included over 40 plant species, with several listed as invasive, such as *Acacia dealbata*, *Carpobrotus edulis*, and *Oxalis pes-caprae*, and others considered to have known ecological risk (either in the early stages of invasion or having a high potential to become invasive in the future), such as *Ludwigia peploides*, *R. japonica*, and *Senecio inaequidens*. This legislation and associated species list were updated by Decree-Law No. 92/2019 (Ministério do Ambiente e Transição Energética 2019), which now includes more than 100 plant species listed as invasive for mainland Portugal. The updated list includes confirmed and potential invasive species known to occur in the territory, as well as others that are presumed absent but expected to become invasive if introduced. Additionally, the European Union Regulation No. 1143/2014 (Official Journal of the European Union 2014) includes the "Union list," which specifically lists the invasive species of Union concern. This regulation aims to prevent and mitigate negative environmental impacts on European Union countries. Species listed are automatically part of the Portuguese national list, being subject to Decree-Law No. 92/2019. As of the third update of the Union list in 2022, 41 plant species are listed (Official Journal of the European Union 2022).

Over the years, a relevant number of studies have investigated plant invasions in Portugal (Sousa et al. 2018). For example, several have listed the diversity of alien plants (Almeida and Freitas 2000; Almeida and Freitas 2012; Marchante et al. 2014), distribution, or potential invasion risk (Rodríguez-Merino 2023). Others have analyzed individual species such as *Baccharis spicata* (Verloove et al. 2017), *C. edulis* (Maltez-Mouro et al. 2009; Chefaoui and Chozas 2019), *Cotula coronopifolia* (Costa et al. 2009), or *Pontederia crassipes* (Pádua et al. 2022a, 2022b; Mouta et al. 2023). Studies have also focused on *Acacia* species (Marchante et al. 2003; Martins et al. 2016; Vicente et al. 2019; Raposo et al. 2021; Große-Stoltenberg et al. 2023), a highly problematic group of taxa due to their invasive behavior, with nine species already established in the territory (Marchante et al. 2023).

Specific regions and ecosystems have also received particular attention, including protected areas (Gutierres et al. 2011; Duarte et al. 2023), dune habitats (Duarte et al. 2023), forests (Ferreira et al. 2021), riparian systems (Bernez et al. 2005; Aguiar and Ferreira 2013; Pabst et al. 2022), and inland waters (Oficialdegui et al. 2023).

Despite the numerous valuable contributions and the growing number of citizen science distribution records on different platforms (e.g., the project "Invasoras.pt" at iNaturalist), the overall distribution of invasive plants across mainland Portugal remains largely unknown. This gap persists despite national inventories of invasive species being essential tools for monitoring invasions, guiding policy, and formulating management plans (Latombe et al. 2017; Pabst et al. 2022; Sirbu et al. 2022). The lack of comprehensive distribution data is likely due, in part, to information on individual taxa being dispersed across numerous sources, making collation and mapping a resource-intensive and challenging task. Additionally, for many species, information about distribution at local scales is incomplete or missing.

Here, we present a comprehensive atlas of the distribution of invasive plant richness in mainland Portugal. This atlas was created by compiling and harmonizing data from a wide range of sources, including national and international biodiversity observation databases, scientific literature, and data collections from managers and researchers. In Portugal, municipalities play a central role in territorial management, environmental planning, and decision-making regarding field interventions. This is also the case for local- and national-level resource allocation for invasive species prevention and management, citizen science initiatives, and public awareness campaigns. Hence, municipalities were selected as reference sampling units. With the information collected, we aimed to: i) map the recorded distribution of each invasive alien plant species in the territory; ii) identify species sharing similar distribution patterns; iii) assess spatial patterns of invasive species richness; and iv) evaluate the environmental and socio-economic drivers of spatial variation in invasive species richness values. Our results are expected to provide substantial support for decision-making in local-to-national-scale prevention and management efforts of alien plant invasions in Portugal.

Materials and methods

Study area

Mainland Portugal is located in the western Iberian Peninsula, at the southwestern edge of Europe (Fig. 1). Its territory spans both the Atlantic and Mediterranean biogeographical regions (Roekaerts 2002). The central and the southern regions (Alentejo and Algarve) are characterized by a Mediterranean climate with dry, hot summers, while the northern regions experience a temperate oceanic climate with dry, mild summers (Beck et al. 2023). The southern and coastal areas are generally low-lying, whereas the northern and central regions are more mountainous, with several peaks exceeding 1,000 m in elevation (Ramos and Ramos-Pereira 2020). The territory is divided into 278 municipalities. The population is primarily concentrated in coastal municipalities, particularly in the metropolitan areas of Lisbon and Oporto (Instituto Nacional de Estatística 2022). Forests occupy large areas in all Nomenclature of Territorial Units for Statistics II (NUTS II) regions, especially in the Centre region, while agricultural areas are most represented in Alentejo and the Lisbon Metropolitan Area (Alves et al. 2022).

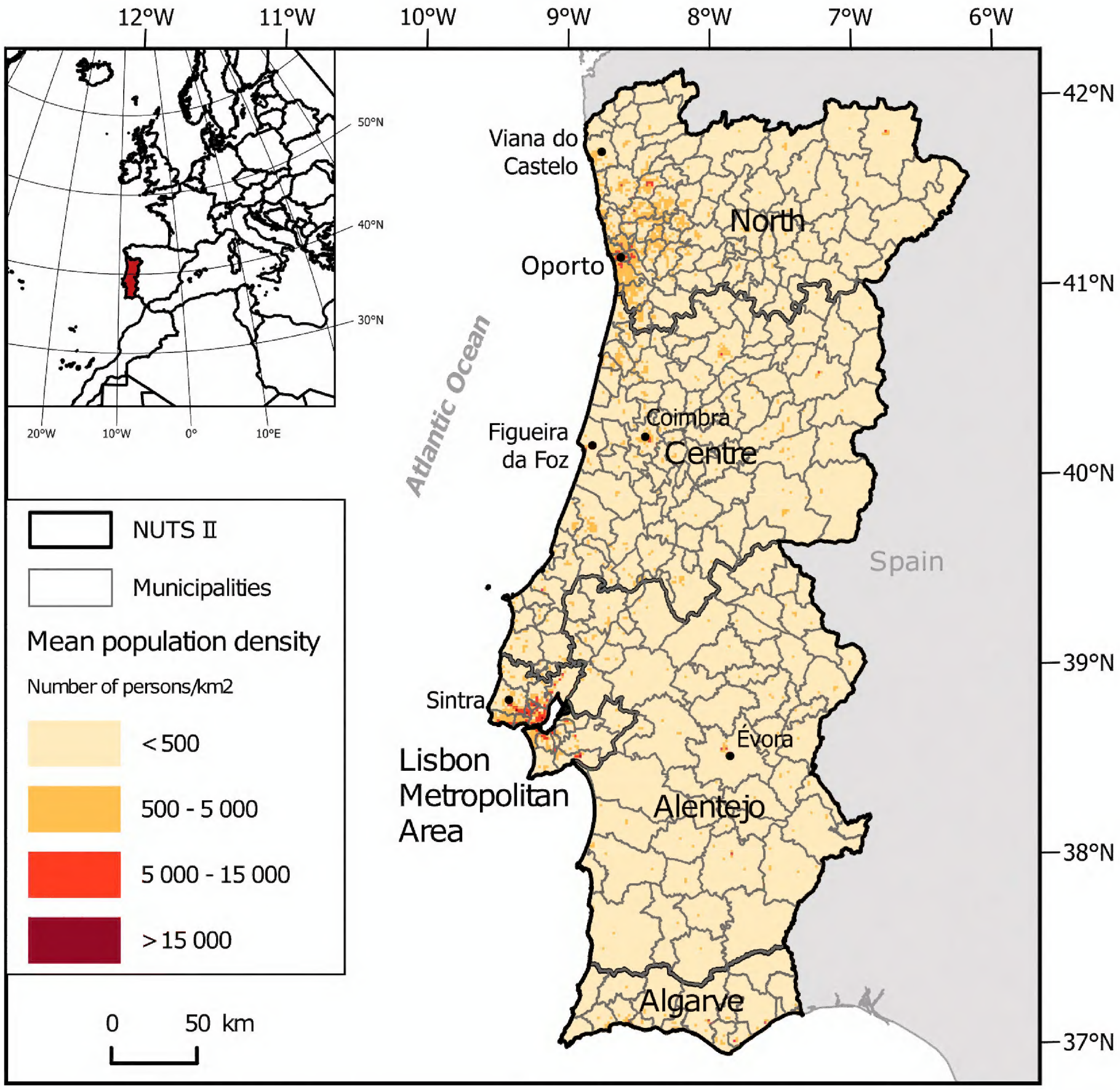


Figure 1. Location of mainland Portugal showing its administrative divisions, including NUTS II regions (outlined in black) and the 278 municipalities (outlined in grey), used as units of analysis in this study. Population density (persons/km^2) is highest in the Lisbon and Oporto Metropolitan Areas, represented by dark red regions.

List of invasive plants

The mapping effort focused on the plant species listed in Portuguese Decree-Law No. 92/2019 (Ministério do Ambiente e Transição Energética 2019) and European Regulation No. 1143/2014 (Official Journal of the European Union 2014). Since our focus is on mainland Portugal, species mentioned in national legislation that pertain only to the insular regions, such as the Madeira archipelago, were excluded. Portuguese Decree-Law No. 92/2019 lists the genus *Acacia* collectively, unlike other taxa, which are listed at the species level. Therefore, we consulted relevant literature (Marchante et al. 2014, 2023) to identify the *Acacia* species known to occur in the territory. Additionally, we included *Watsonia meriana* in our mapping, as the research community recognizes its invasive behavior in several areas of mainland Portugal (Marchante et al. 2014; Morais et al. 2017). Distribution data were collected for a total of 96 species from 64 different genera (Suppl. material 1: table S1.1).

Occurrence database

We gathered occurrence records for each invasive plant species from multiple sources. The online databases consulted included the Global Biodiversity Information Facility (GBIF) (GBIF.org 2024); Flora-On (Flora de Portugal Interactiva 2024), an expert-led project aimed at systematizing information for all vascular plant species in Portugal, including their distribution; and the citizen-science platforms iNaturalist (iNaturalist 2024) (only research-grade records were considered) and Pl@ntNet (Pl@ntNet 2024). Records were also collected from numerous research publications identified in Web of Science and Scopus using the search terms "Portugal" and each species name, as well as from master's and doctoral theses identified in RENATES, a Portuguese platform containing official information on dissertations produced in Portugal (DGEEC 2024). Additionally, we incorporated unpublished data from the authors, collaborators, and companies involved in invasive plant management actions (see Acknowledgments section). Data up to May 2024 were considered.

The taxonomy of species was defined and harmonized according to the GBIF Backbone Taxonomy (GBIF Secretariat 2023). Occurrence records were collected for all available years and included subspecies (if present). Records identified as having coordinates of stored specimens (e.g., herbarium locations) rather than the actual place of observation in the wild were removed. Additionally, records with a spatial precision of less than 100 m were excluded.

An exception was made for data from Flora-On. This source is crucial for the comprehensiveness of the mapping but provides data as centroids of grid squares at a 10 × 10 km resolution. Despite its contribution to spatial comprehensiveness, the lower geographical precision may introduce some spatial errors in attributing occurrences to municipalities—the spatial units of mapping and analysis used (see below). Therefore, we performed two mapping exercises and associated analyses: one including Flora-On data and another without it. The results from both datasets were highly congruent (see Results section). Thus, we primarily describe the results, including the entire set of occurrence data, while those excluding Flora-On data are provided in Suppl. material 3.

Given the breadth of consulted sources, we expect to have obtained a representative identification of the species occurring in each municipality. However, as with any similar exercise, our data may still exhibit some gaps and biases, particularly toward regions with higher recording efforts and species that are more conspicuous and easier to identify (see Discussion section for details).

Invasive plant richness mapping and occupancy

To analyze species distribution patterns, we aggregated occurrence records at the municipality level, following the boundaries defined by the Carta Administrativa Oficial de Portugal (CAOP) (Direção-Geral do Território 2024). For each municipality, duplicate records of the same species were removed, retaining only one occurrence per species. Invasive species richness was then calculated as the total number of unique species recorded per municipality. Species occupancy patterns were assessed by quantifying, within each municipality, the number of 1 × 1 km grid cells in which the species was recorded. The mean percentage of occupied grid cells across municipalities was subsequently calculated to represent overall species occupancy. Analyses were performed in R v4.3.2 (R Core Team 2022).

Assessing patterns of species distributions

To identify similarities in species-level patterns of distribution across the territory, we first characterized the distribution of each species using five variables: the number of municipalities where occurs; the median and interquartile range of distance to the coast (from the centroid of each municipality, in kilometers); and the median and interquartile range of latitude (in decimal degrees).

We then performed a cluster analysis based on these variables. To account for multicollinearity among the variables, we used principal component analysis (PCA), which explained 72.3% of the variance with the first two components (Suppl. material 1: fig. S1.1). Next, we performed a k-means clustering analysis based on the scores of each species in the two-dimensional PCA space. The PCA was performed using the "prcomp" function from the *stats* R package. The k-means procedure employed the "kmeans" function from the same package, and the elbow method (Bholowalia and Kumar 2014) was used to identify the optimal number of clusters (Suppl. material 1: fig. S1.2).

We also examined whether the number of municipalities where a species occurs reflects its overall occupancy across the territory. To do this, we fitted a linear model relating the mean occupancy of species (i.e., the average percentage of occupied 1 × 1 km grid cells per municipality) to the total number of municipalities where it was recorded.

Spatial drivers of invasive plant richness

Explanatory variables

To identify the factors driving the spatial variation in the richness of invasive plants across the territory, we selected a comprehensive set of 30 variables (Table 1) representing distinct environmental and human-related factors, including proxies for recording effort. These variables were mapped at the municipality level and provide a broad representation of the hypotheses on driving factors considered in previous studies (Vicente et al. 2010; Santos et al. 2011; Vicente et al. 2019; Vieites-Blanco and González-Prieto 2020; Pabst et al. 2022).

The variables representing climatic conditions, topography, continentality, socioeconomy (gross domestic product [GDP] and travel time to cities, i.e., the time it takes to travel to the nearest urban center via surface transport) (Weiss et al. 2018), and soil groups consisted of mean values of raster cell data within the boundaries of each municipality. The land-use variables used vector-type base data and were obtained by dividing the total area occupied by each land-use class by the municipality's total area. Additionally, variables representing dispersal corridors were calculated by summing the extent of these entities (hydrographic network, road infrastructure, railways, and power lines) within each municipality and dividing by its area. The minimum distance to the coastline was determined as the shortest distance from the centroid of each municipality.

The availability of species distribution data can be strongly influenced by varying levels of recording effort (Tiago et al. 2017). Therefore, we considered a set of variables expected to represent spatial patterns in this effort across the territory. These variables were the average number of higher education students per municipality, the number of higher education institutions per

Table 1. Explanatory variables considered as predictors of spatial variation patterns of invasive plant richness. The final set of variables (in bold) was determined after assessing multicollinearity.

Group	Variables	Transformation	Source	VIF
Climate	Annual precipitation amount (kg m^{-2})		Chelsa (1981–2010) (Karger et al. 2017, 2018)	>5
	Precipitation amount of the wettest month (kg m^{-2})			>5
	Precipitation amount of the driest month (kg m^{-2})			>5
	Annual mean temperature (°C)			>5
	Daily mean air temperatures of the driest quarter (°C)			>5
	Daily mean air temperatures of the wettest quarter (°C)			**3.44**
	Daily mean air temperatures of the coldest quarter (°C)			>5
	Mean daily maximum air temperature of the warmest month (°C)			**2.38**
	Mean daily minimum air temperature of the coldest month (°C)			>5
Topography	Slope (degrees)		Earth Resources Observation and Science (EROS) Center (2018)	>5
	Elevation (meters)			>5
	Ruggedness Index			**3.06**
Geography	**Minimum distance to coastline (km)**			**2.58**
	Municipality area (km^2)	Sqrt	Direção-Geral do Território (2024)	**2.55**
Land use	Density of artificialized territories (%)	Log(x+1)	COS, Version 2018 (Direção Geral do Território (DGT), 2020)	>5
	Density of agricultural areas (%)			**2.02**
	Density of forest areas (%)			**2.70**
	Density of protected areas (%)	Log(x+1)	Instituto da Conservação da Natureza e das Florestas (ICNF) (2022, 2023a, 2023b, 2023c, 2023d)	**1.89**
	Burnt area (2007–2022) (%)		Instituto da Conservação da Natureza e das Florestas (ICNF) (2024)	**2.65**
Soil	**Average soil pH (15–30 cm layer)**	Log	Poggio et al. (2021)	**2.32**
Density of dispersal corridors	**Density of local hydrographic network (km/km^2) (2024)**		OpenStreetMap. Geofabrik GmbH, and OpenStreetMap Contributors (2018)	**2.13**
	Density of roads (km/km^2) (2024)	Log(x+1)		>5
	Density of railways (km/km^2) (2024)	Log(x+1)		**1.92**
	Density of power lines (km/km^2) (2024)	Log(x+1)	REN—Redes Energéticas Nacionais, SA (see acknowledgments)	**1.26**
Socioeconomic	Mean population density according to the national census (mean value of 2001, 2011, and 2021; number of persons/km^2)	Log	INE, PORDATA (2024)	>5
	GDP (1990–2015; 2011 international US dollars)	Log	Kummu et al. (2015)	>5
	Travel time to cities (minutes)		Weiss et al. (2018)	**2.97**
	Sampling effort (academic and citizen-science sampling effort)		DGEEC/ME-MCTE, PORDATA (2021, 2024); INE, PORDATA (2024)	**3.21**
	Number of iNaturalist projects with IAP records	Log(x+1)	iNaturalist (2024)	**2.51**
	Number of plant nurseries and aquarium stores	Log(x+1)	Nunes et al. (unpublished)	**1.69**

municipality, and the number of iNaturalist projects with invasive plant records per municipality. To avoid redundancy in their spatial variation, we projected these variables into a PCA. The first principal component, explaining around 75% of the variance, was retained, representing mainly the joint variation of the number of higher education students and institutions. The scores of this first composite were extracted and used as a new variable named "academic sampling effort" (Table 1). Because the number of iNaturalist projects contributed little to this component, we used the original values of this variable as a proxy for "citizen-science sampling effort".

Testing for drivers of invasive plant richness

To assess the relationship between the richness of invasive plants across the territory (dependent variable) and the explanatory variables (Table 1), we used a generalized least squares (GLS) regression model (Dormann et al. 2007). Prior to model fitting, square root and logarithmic transformations were applied to several explanatory variables (Table 1). The response variable was also log-transformed to meet model expectations of a Gaussian distribution of error (Ives 2015).

Potential multicollinearity among the explanatory variables was assessed using the variance inflation factor (VIF) (Alin 2010), calculated with the "vifstep" function from the *usdm* R package (Naimi 2022). Only the set of explanatory variables with a VIF < 5 was considered for the GLS model (Table 1).

This model was fitted using the "gls" function from the *nlme* R package (Pinheiro et al. 2023), assuming an exponential decay in the spatial autocorrelation of richness values (Dormann et al. 2007). Significant relationships between dependent and explanatory variables were determined at $\alpha = 0.05$, and the goodness of fit of the model was measured using the pseudo-R^2 of Nakagawa et al. (2017).

Results

Invasive plants over Portuguese municipalities

Of the 96 invasive plants with distribution records in mainland Portugal (Suppl. material 1: table S1.1), 86% are terrestrial, with a smaller portion being aquatic or semi-aquatic (14%), including plants such as *Alternanthera philoxeroides* and *Ludwigia* spp. They include grasses and herbs (47%), trees and shrubs (29%), and only a few climbing plants (5%) and other growth forms (Suppl. material 1: fig. S1.3). These species belong to 36 plant families, mainly Asteraceae (16%), Amaranthaceae (14%), Fabaceae (14%), and Poaceae (9%) (Suppl. material 1: fig. S1.4).

Of the 10 species with records in the greatest number of municipalities (Table 2), the majority are grasses and herbs (50%; e.g., *Datura stramonium*, *C. selloana*) and trees and shrubs (40%; e.g., *A. dealbata*, *Ailanthus altissima*) (Table 2). Six are already present in more than 200 municipalities (Table 2). The species recorded in only a few municipalities (up to 10; Suppl. material 1: table S1.2) are mostly aquatic or semi-aquatic (40%; e.g., *Nymphaea mexicana* or *Ludwigia grandiflora*).

Table 2. The 10 invasive plants recorded in the greatest number of Portuguese municipalities.

Species	Number of municipalities with records of the species
Acacia dealbata	249
Datura stramonium	233
Arundo donax	232
Phytolacca americana	224
Oxalis pes-caprae	213
Cortaderia selloana	208
Ailanthus altissima	198
Acacia melanoxylon	190
Agave americana	187
Robinia pseudoacacia	186

Four species have been recorded in a single municipality (*A. philoxeroides*, *Amaranthus hypochondriacus*, *Amaranthus muricatus*, and *Baccharis halimifolia*; Suppl. material 1: table S1.2). The distribution of each species per municipality is provided in Suppl. material 4.

The three species with the highest mean percentage of occupancy in mainland Portugal—*O. pes-caprae* (7.53%), *Arundo donax* (6.90%), and *C. selloana* (6.87%)—are also among the most widely distributed, occurring in more than 200 municipalities (Table 2, Suppl. material 1: table S1.3). Their broad geographic range reflects both high local presence and widespread dispersal across the country. In contrast, *Arctotheca calendula* (5.88%) and *Acacia longifolia* (5.58%) rank fourth and fifth in mean occupancy but have a more restricted national distribution. Their presence is concentrated in coastal regions, suggesting high local abundance but limited expansion at a broader scale (Suppl. material 1: table S1.3).

Similarly, the regression model assessing the relationship between the number of municipalities in which a species was recorded and its mean occupancy revealed a statistically significant positive association ($p < 0.05$), explaining 42% of the observed variation. This suggests that species occurring in a greater number of municipalities also tend to occupy larger areas within those municipalities. However, the substantial unexplained variation indicates that additional factors influence species occupancy patterns (Fig. 2).

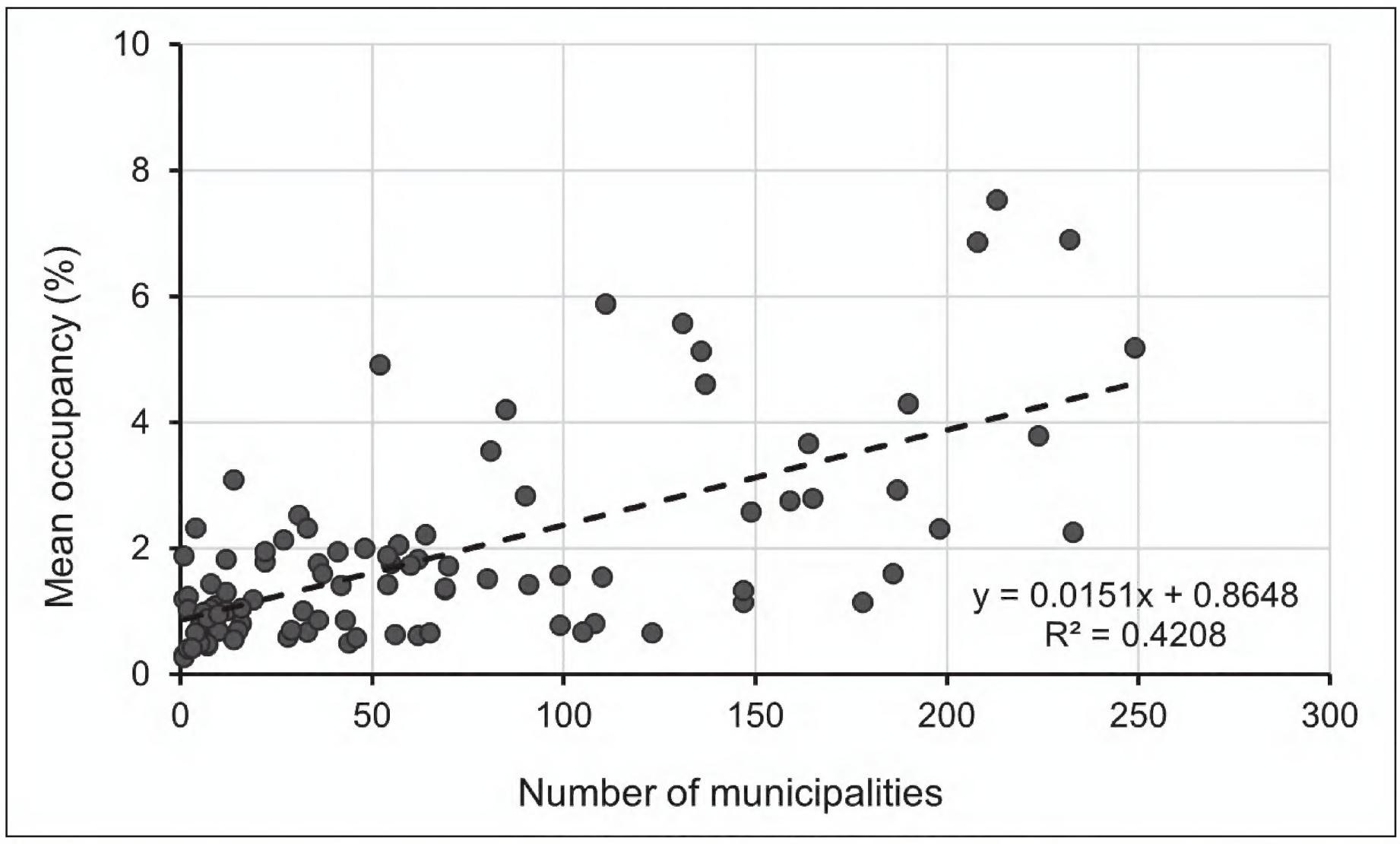


Figure 2. Linear regression model showing the relationship between the total number of municipalities where each species was recorded and its average occupancy (%). Each dot represents a species. The dashed line indicates the fitted linear relationship.

Distribution patterns of invasive plant richness

Overall, the species are grouped into four distinct clusters (Fig. 3, Suppl. materials 1, 3: table S1.4, fig. S3.1). The first cluster (Fig. 3) includes 26 species predominantly recorded in coastal areas, such as *A. saligna* (Fig. 4a) and *C. coronopifolia*.

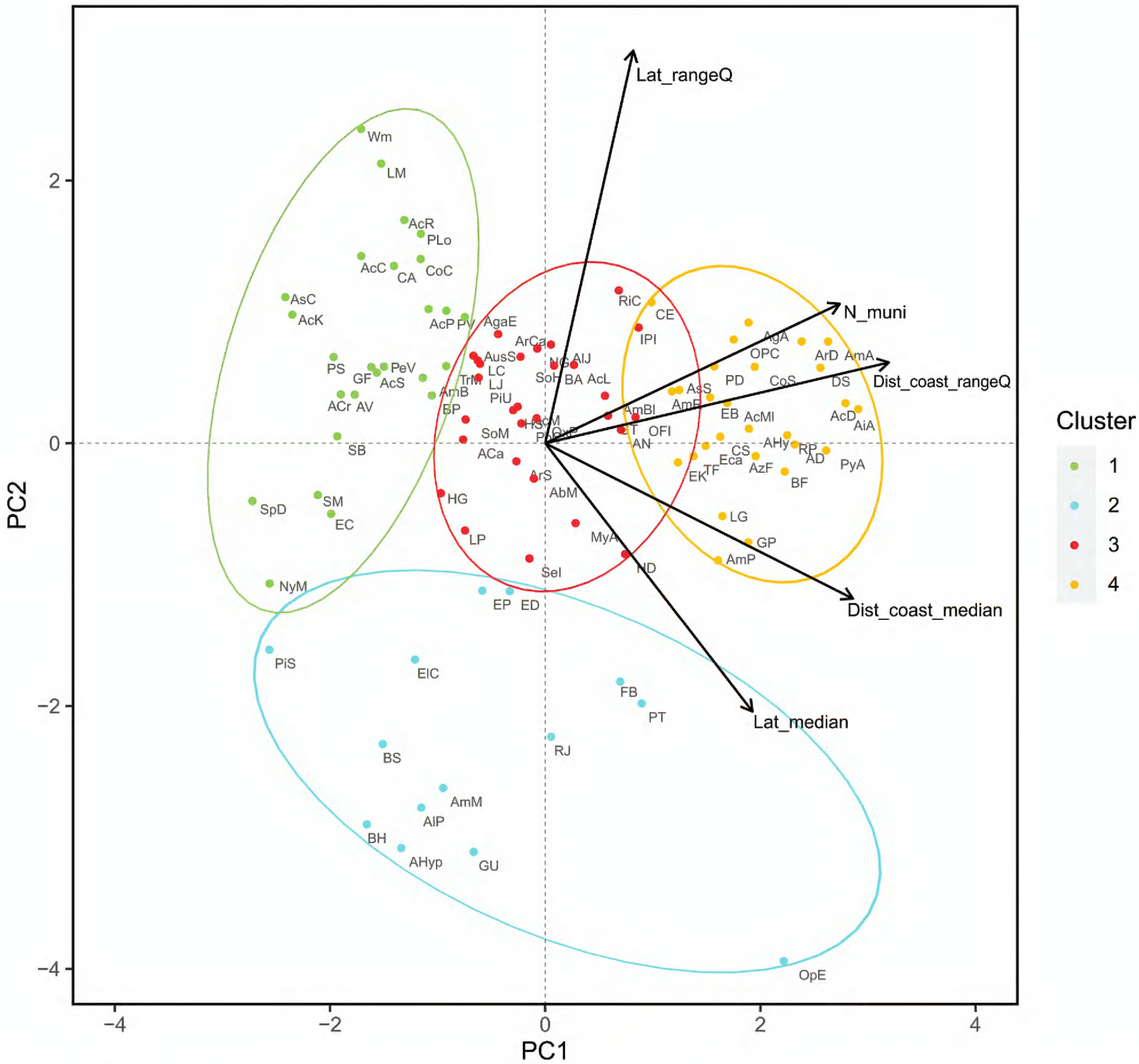
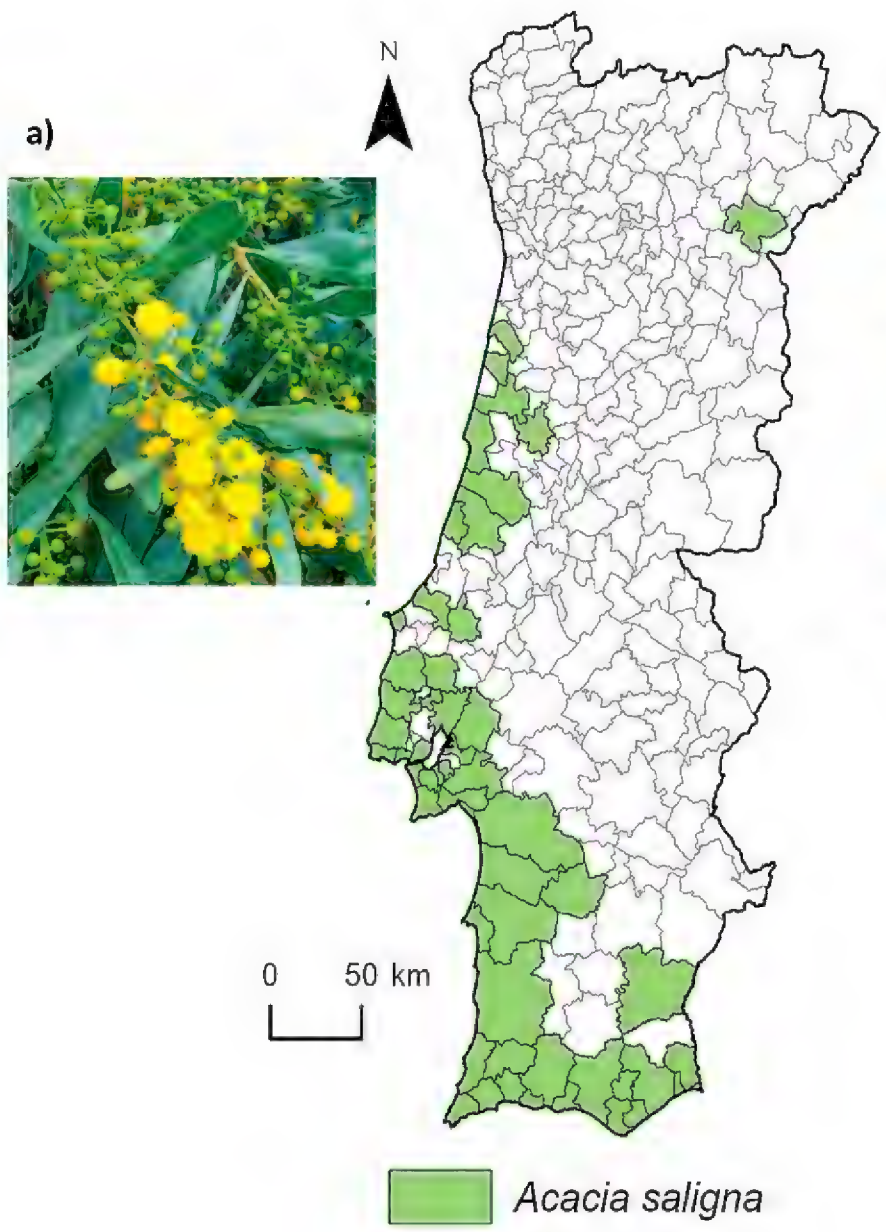
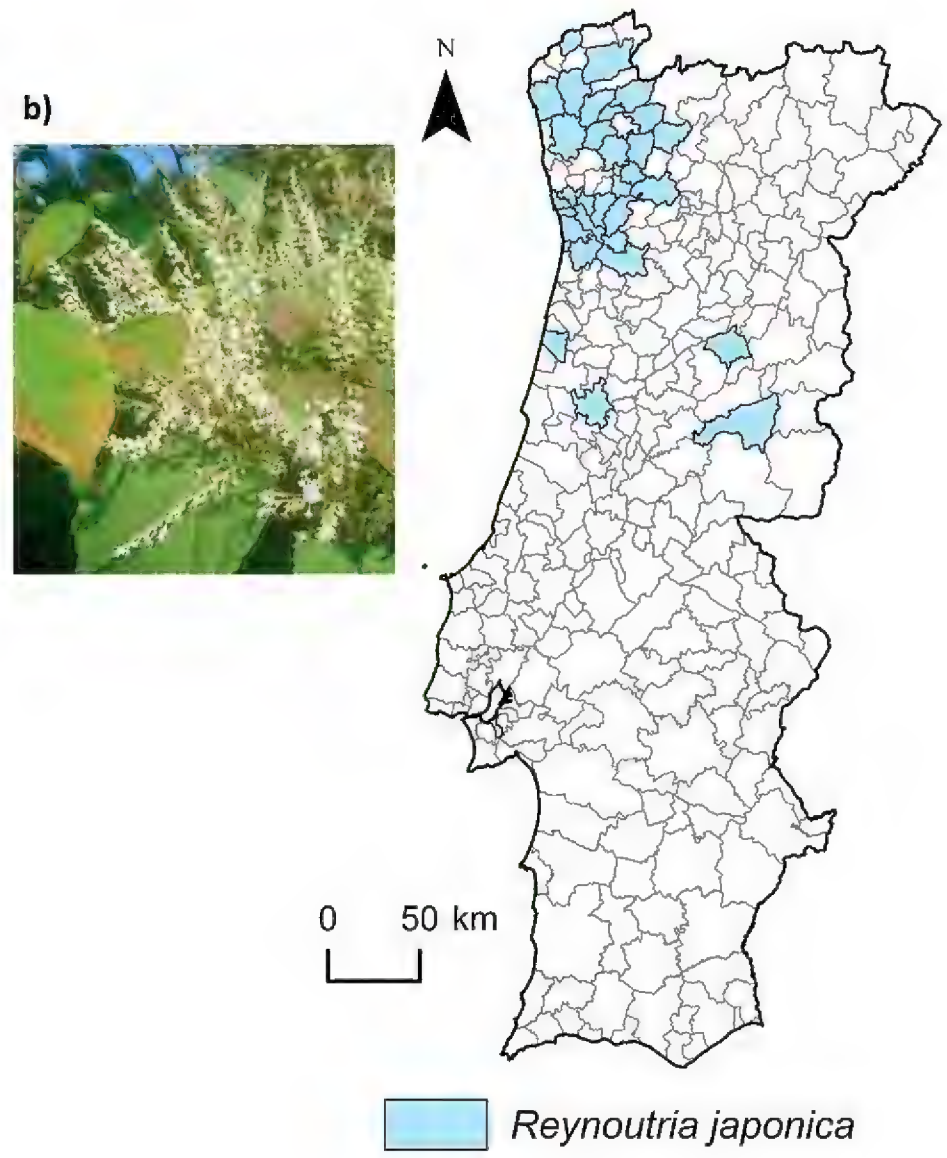
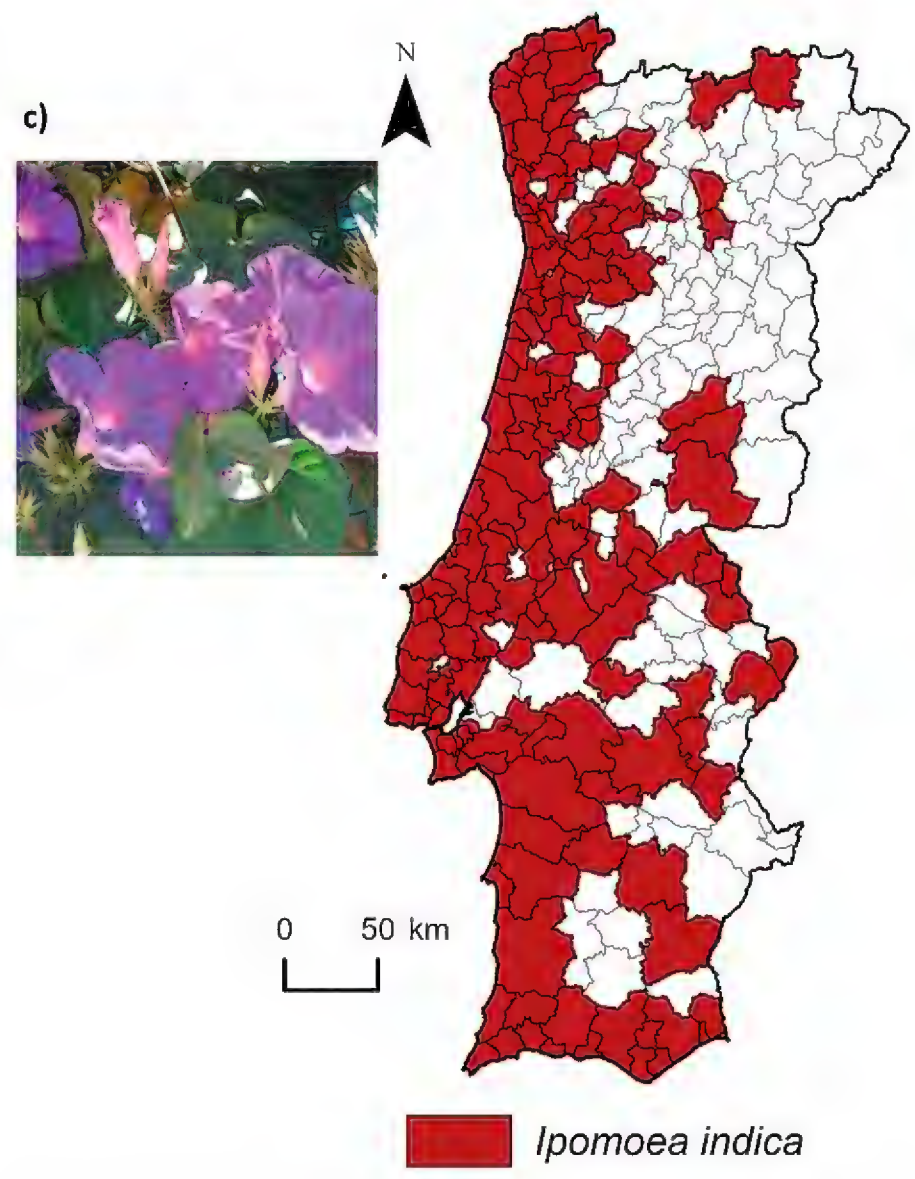


Figure 3. Clusters of invasive plants according to their distribution patterns in mainland Portugal. Cluster 1 (green): species primarily located along the coast; Cluster 2 (blue): mostly species with narrow ranges; Cluster 3 (red): moderately widespread species; Cluster 4 (yellow): mostly widespread species. The two PCA axes represent variation in the total number of municipalities of occurrence (N_muni), the median distance to the coast (Dist_coast_median), the interquartile range of distances to the coast (Dist_coast_rangeQ), the median latitude (Lat_median), and the interquartile range of latitudes (Lat_rangeQ).

The remaining three groups are differentiated mainly by the breadth of their distribution ranges. The second cluster includes 14 species characterized by narrow distribution areas (up to 33 municipalities). These species are also generally found in central and northern municipalities (e.g., *R. japonica*, Fig. 4b, and *B. halimifolia*). The third cluster includes 29 mostly moderately widespread species (e.g., *A. longifolia* and *I. indica*, Fig. 4c). Although there are 10 species with narrow distributions (up to 33 municipalities; Suppl. material 1: table S1.4), they were grouped in the third cluster because of their wider latitudinal range than those in the second cluster. The final group consists of 27 species, mostly with very wide ranges (mean number of municipalities = 145 ± 67). Examples of species included in this last group are *A. dealbata* and *C. selloana* (Fig. 4d).







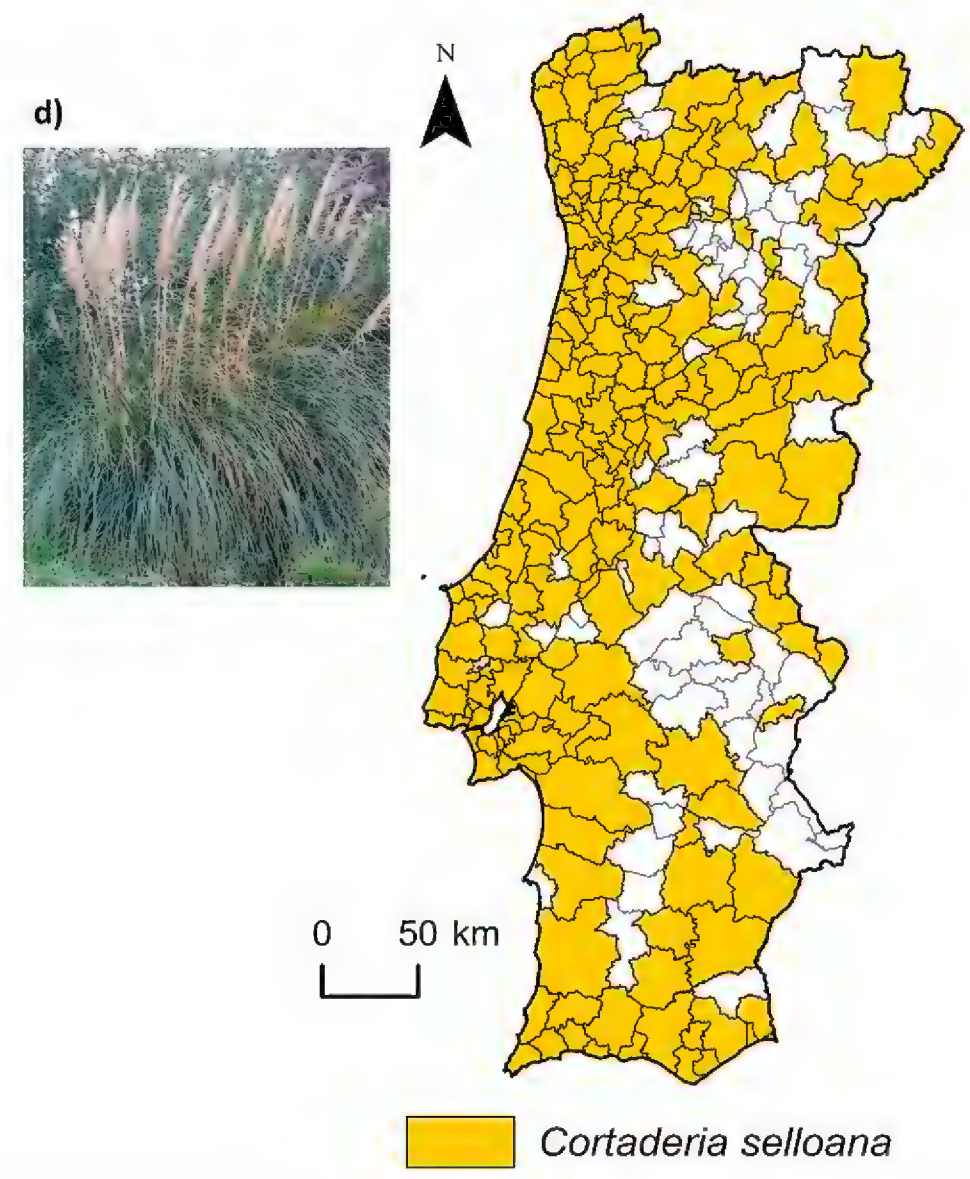


Figure 4. Distribution of example species within each cluster, grouped according to the k-means clustering (Fig. 3) across the Portuguese territory: **a.** Cluster 1 (green)—*Acacia saligna*; **b.** Cluster 2 (blue)—*Reynoutria japonica*; **c.** Cluster 3 (dark red)—*Ipomoea indica*; **d.** Cluster 4 (yellow)—*Cortaderia selloana*.

Patterns and drivers of invasive plant richness

At least one invasive plant species has been recorded in each Portuguese municipality (Fig. 5, Suppl. material 3: fig. S3.2). Richness is markedly higher in coastal municipalities, particularly those near major urban centers such as the metropolitan areas of Lisbon and Oporto. Additionally, certain cities of regional significance, including Coimbra, Figueira da Foz, and Viana do Castelo, as well as locations along the Algarve coast in southern Portugal, also exhibit high numbers of invasive plants. The highest numbers were recorded in Lisbon (63 species), Coimbra (62), Sintra (58), and Figueira da Foz (55). Conversely, lower richness was observed in municipalities located primarily in northeastern Portugal and in some central and inland regions of Alentejo.

The GLS model identified drivers of variation in invasive species richness, achieving a pseudo-R^2 value of 0.59, indicating good explanatory capacity. Four variables exhibited significant relationships with richness values ($p < 0.05$; Table 3, Suppl. material 3: table S3.1). Specifically, invasive species richness increased with larger municipality area, higher density of power lines, greater proximity to the coastline, and shorter travel time to cities.

Table 3. Coefficients and *p*-value results of each explanatory variable considered in the GLS model. Significant relationships ($p < 0.05$) with variation in invasive plant richness by municipality are shown in bold.

Explanatory variable	Coefficient (SE)	*p*-value
Precipitation amount of the wettest month (kg m-2)	-0.0009 (0.001)	0.103
Mean daily maximum air temperature of the warmest month (°C)	-0.0323 (0.029)	0.259
Ruggedness Index	0.0105 (0.010)	0.272
Minimum distance to coastline	**-0.0074 (0.002)**	**0.003**
Municipality area	**0.0478 (0.006)**	**<.001**
Density of agricultural areas	0.0014 (0.003)	0.606
Density of forest areas	0.0005 (0.003)	0.86
Density of protected areas	0.0270 (0.015)	0.077
Burnt area in the last 15 years	0.0004 (0.002)	0.868
Soil pH	0.7854 (1.176)	0.505
Density of local hydrographic network	0.0680 (0.090)	0.449
Density of railways	0.1167 (0.154)	0.448
Density of power lines	**0.4782 (0.231)**	**0.039**
Travel time to cities (minutes)	**-0.0070 (0.002)**	**0.003**
Sampling effort (academic and citizen-science sampling effort)	0.0445 (0.025)	0.071
Number of iNaturalist projects with IAP records	0.1681 (0.189)	0.374
Number of plant nurseries and aquarium stores	0.0778 (0.045)	0.082

Discussion

Our assessment reveals that invasive alien plant species are now established throughout mainland Portugal, yet their patterns of distribution and occupancy are far from uniform. By integrating approximately 85,000 occurrence records from multiple sources, we identified the distribution of 96 invasive plant species across the study area. While previous works estimated the number of invasive alien plants occurring in the country (Almeida and Freitas 2000; Almeida and Freitas 2012; Morais et al. 2017), they did not assess their spatial distribution at the national scale. Other studies examined nationwide distribution patterns but focused on single species (e.g., González et al. 2020). This study provides new insights into the distribution of invasive plant species and their richness in mainland Portugal.

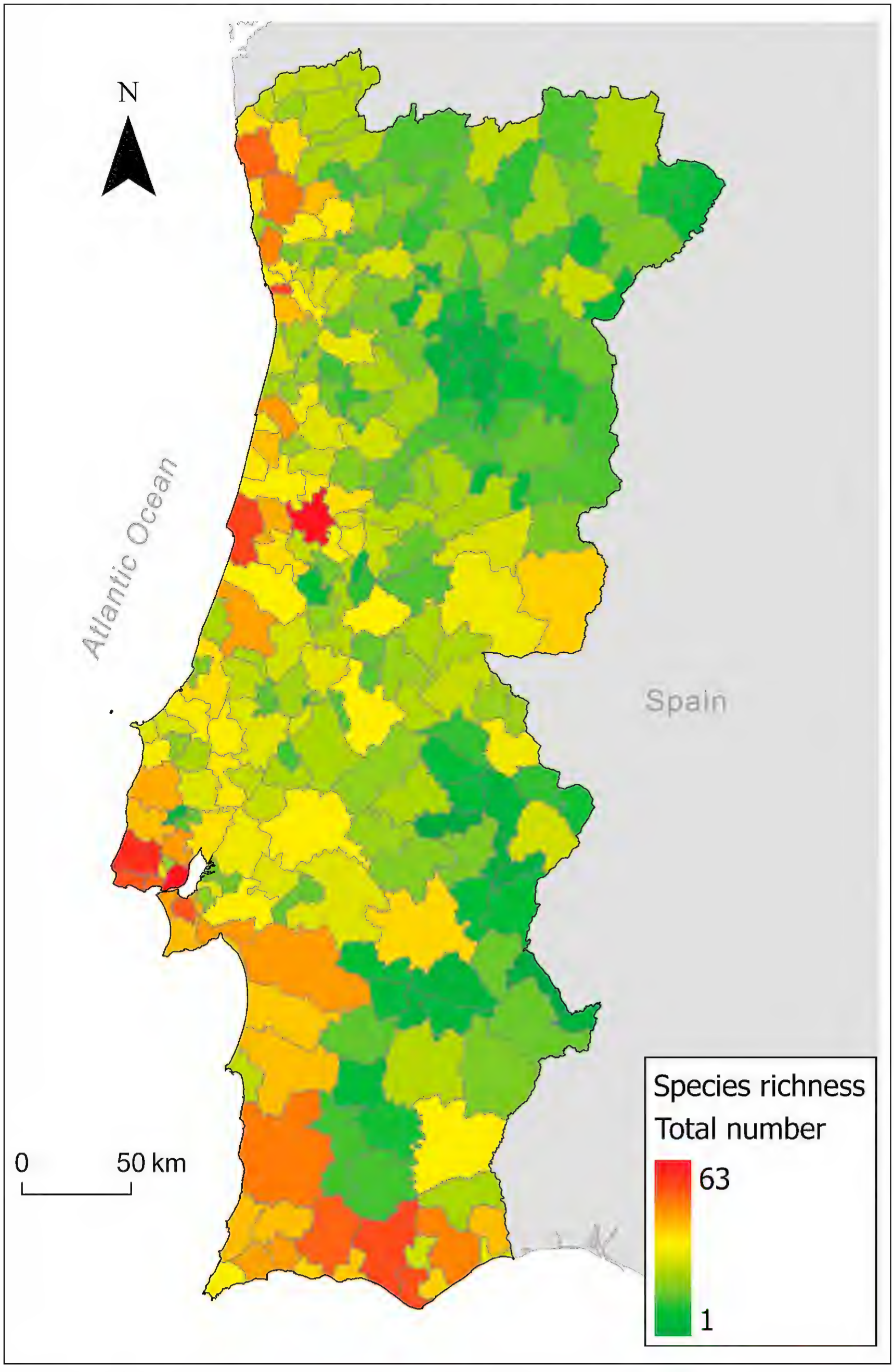


Figure 5. Richness of invasive alien plant species in mainland Portugal, corresponding to the total number of these species recorded in each municipality.

Spatial patterns of invasive species richness

Coastal and urbanized areas, particularly around Lisbon, Oporto, and the Algarve, emerge as hotspots of invasive species richness. In contrast, inland and northeastern regions remain less heavily invaded. Proximity to the coastline and shorter travel times to urban centers were identified as significant predictors of invasive species richness, reinforcing the role of urbanization, human disturbance, and accessibility in driving invasions as favorable conditions for the introduction, establishment, and spread of alien species in many regions (e.g., Pyšek and Richardson 2010; Santos et al. 2011; Dawson et al. 2017; Pyšek et al. 2020; Dimitrakopoulos et al. 2022; Polce et al. 2023; Musarella et al. 2024; Ivison et al. 2025; Montagnani et al. 2025). This reflects the demographic and economic structure of Portugal, which is strongly coast-biased, with population and related activities concentrated along the western and southern coastal regions, particularly in and around the Lisbon and Oporto metropolitan areas (Instituto Nacional de Estatística 2022). Some widespread invasive species in Portugal are known to have been initially brought to major urban centers as ornamentals (e.g., *I. indica* or *Erigeron karvinskianus*; Marchante et al. 2014), while others were introduced specifically to coastal ecosystems in past decades, especially for dune fixation and erosion control (e.g., *A. longifolia* or *C. edulis*; Marchante et al. 2014).

Invasive species richness was also positively associated with municipality size and the density of power-line corridors. The effect of area aligns with the classic species–area relationship, whereby larger spatial units tend to encompass a greater variety of habitats and a broader representation of the regional species pool, supporting more stable and abundant populations and contributing to higher observed species richness (Matthews et al. 2021). On the other hand, linear infrastructures such as power lines may function as ecological corridors. These areas are subject to vegetation cutting interventions, which cause disturbance and eliminate competition—factors known to facilitate the dispersal and establishment of invasive plant species (Dalu et al. 2023). Despite this, the role of such linear infrastructures in plant invasion in Portugal remains underexplored.

Although climate is a known driver of alien species distributions (Dutra Silva et al. 2021), climatic variables were not significant predictors of invasive plant richness in this study. This may reflect the stronger influence of anthropogenic factors, namely human distribution and activities. Moreover, despite its relatively small size globally, mainland Portugal presents relatively diverse climatic conditions, shaped largely by its latitudinal gradient, with warmer, dry Mediterranean-type climates in southern regions and cooler, humid temperate climates in northern coastal areas (Beck et al. 2023). We anticipated a significant relationship between soil pH and invasive species richness, given that calcareous and serpentinic soils—known for their high pH and challenging chemical profiles—tend to support fewer invasive plants. However, this expected effect may have been obscured because municipality-level pH values represent averages across diverse soil types, thereby diluting the influence of localized extremes.

Further insights emerged from the cluster analysis (Fig. 3), which revealed four main distribution patterns ranging from narrowly confined inland species to widely distributed taxa spanning both latitudinal and coastal–inland gradients. While most species conformed to expected patterns, notable exceptions emerged (e.g., *C. selloana*, which was classified as widespread, is relatively uncommon in inland regions; González et al. 2020). This highlights how presence-only data at the municipal level may obscure finer-scale spatial variation.

These spatial and ecological patterns carry critical implications for monitoring and management. Species recorded in only a few but geographically dispersed municipalities, such as *L. grandiflora*, may reflect either early-stage invasions or underreporting. Differentiating between these scenarios is crucial, as early detection offers a window of opportunity for effective containment or eradication. Targeted field surveys and systematic monitoring should prioritize such cases to reduce uncertainty and support timely interventions.

Finally, the analysis revealed a moderate positive association ($R^2 = 0.42$) between the number of municipalities in which a species occurs and its mean occupancy, suggesting that widespread species are also more likely to be locally dominant. This is evident for well-established invaders such as *A. dealbata*, *A. donax*, *O. pes-caprae*, and *Phytolacca americana*, whose ecological impacts in mainland Portugal are well documented (Aguiar and Ferreira 2013; Castro et al. 2016; Duarte et al. 2020; Marchante et al. 2023). In contrast, some species, such as *A. longifolia*, *A. saligna*, and *C. edulis*, show high local occupancy but limited national spread (mainly in coastal dune areas; Marchante et al. 2014), suggesting environmentally constrained yet intense localized invasions.

Species richness as an indicator: opportunities and limitations

The measure of invasive species richness, derived from municipality-level presence data, provides a valuable and standardized overview of invasive plant distributions across mainland Portugal. While this approach does not capture local abundance—which could offer further insight into ecological dominance and impact—it remains a practical method for identifying general patterns of invasion. As with many large-scale biodiversity assessments, the underlying data are primarily sourced from opportunistic records, including citizen-science contributions. Although these sources provide broad spatial coverage and large volumes of data, they can introduce spatial biases related to observer effort, site accessibility, and species detectability (Isaac et al. 2014; Tiago et al. 2017; Westekemper et al. 2018). As a result, the apparent absence of species in certain areas may reflect lower sampling effort rather than true absence, particularly for less conspicuous or recently introduced taxa.

Moreover, invasive species richness does not differentiate among species in terms of their ecological impact or management urgency. For example, the detection of *Fallopia japonica* in a new location may warrant immediate action due to its known severe ecological consequences (Aguilera et al. 2010), while a new occurrence of *E. karvinskianus* might pose a more localized and manageable concern. While our analysis adopts an equal-weight approach across species, it establishes a foundational framework that can be enhanced through species-specific risk assessments and prioritization strategies, which are vital for informed resource allocation and targeted management.

Despite limitations inherent in opportunistic and citizen-science data (Robinson et al. 2017), these data offer a cost-effective way to collect species records in greater numbers and at more locations. Moreover, using invasive species richness as a pressure indicator is a helpful tool to identify areas where conservation and management efforts should be prioritized (Fleishman et al. 2006; Santos et al. 2011). However, while it is a useful tool for spotting potential invasion hotspots, it should not be interpreted as a direct measure of invasion severity or ecological impact.

Conclusion

This study provides insights into the spatial patterns and environmental and human drivers of invasive plant richness in mainland Portuguese municipalities. Coastal urban areas show the highest invasive species richness, largely driven by greater accessibility. This suggests that municipalities in these regions should prioritize invasive plant management due to their higher levels of impact. At the same time, municipalities with fewer invasive species must act early to prevent their spread, thereby increasing the effectiveness and sustainability of management efforts nationwide. Despite relying on the total number of invasive plants in each municipality, and not their abundance, the results offer a valuable baseline for identifying invasion hotspots and guiding management priorities. Continued monitoring and systematic data collection are essential to support effective prevention and control of plant invasions across the country.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

We used AI to polish the manuscript text and help develop the R code for the methodology.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Results with all occurrence data

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Data type: docx

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Supplementary material 2

Markdown

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Supplementary material 3

Results without FloraOn data

Authors: Raquel Fernandes, Andry Castro, Hélia Marchante, Elizabete Marchante, César Capinha
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Supplementary material 4

Atlas of invasive plant species

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